Current Biology

Report

Evidence that Magnetic Navigation and Geomagnetic Imprinting Shape Spatial Genetic Variation in Sea Turtles

Highlights

- Geomagnetic signatures of nesting beaches predict sea turtle population structure
- Results provide genetic evidence consistent with geomagnetic imprinting in sea turtles
- Findings reveal a new driver of spatial genetic variation
- Similar processes may shape population structure in diverse migratory animals

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In Brief

Brothers and Lohmann report a relationship between sea turtle population structure and Earth's magnetic field. Results provide genetic evidence that turtles accomplish natal homing via magnetic navigation, which can evidently mediate genetic differentiation independent of isolation by distance or environment.

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Report

Evidence that Magnetic Navigation and Geomagnetic Imprinting Shape Spatial Genetic Variation in Sea Turtles

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SUMMARY

The canonical drivers of population genetic structure, or spatial genetic variation, are isolation by distance and isolation by environment. Isolation by distance predicts that neighboring populations will be genetically similar and geographically distant populations will be genetically distinct [1]. Numerous examples also exist of isolation by environment, a phenomenon in which populations that inhabit similar environments (e.g., same elevation, temperature, or vegetation) are genetically similar even if they are distant, whereas populations that inhabit different environments are genetically distinct even when geographically close [2–4]. These dual models provide a widely accepted conceptual framework for understanding population structure [5–8]. Here, we present evidence for an additional, novel process that we call isolation by navigation, in which the navigational mechanism used by a long-distance migrant influences population structure independently of isolation by either distance or environment. Specifically, we investigated the population structure of loggerhead sea turtles (*Caretta caretta*) [9], which return to nest on their natal beaches by seeking out unique magnetic signatures along the coast—a behavior known as geomagnetic imprinting [10–12]. Results reveal that spatial variation in Earth's magnetic field strongly predicts genetic differentiation between nesting beaches, even when environmental similarities and geographic proximity are taken into account. The findings provide genetic corroboration of geomagnetic imprinting [10, 13]. Moreover, they provide strong evidence that geomagnetic imprinting and magnetic navigation help shape the population structure of sea turtles and perhaps numerous other long-distance migrants that return to their natal areas to reproduce [13–17].

RESULTS AND DISCUSSION

Neither of the two classical drivers of population structure readily explains the enigmatic pattern of spatial genetic variation that exists within the largest sea turtle rookery in North America. Specifically, the genetic structure of the loggerhead turtle population in the southeastern United States appears inconsistent with isolation by distance in that turtles nesting on beaches that are relatively close together are often genetically distinct, while those that nest on beaches that are farther apart (including some on the east and west coasts of Florida) are often genetically alike [9]. Similarly, isolation by environment cannot readily account for the pattern, as nesting beaches that are close together but used by genetically distinct populations often appear to be physically identical.

An interesting possibility is that the unusual genetic structure arises through a mechanism involving navigation to natal beaches [9, 12]. After departing from their natal beaches as hatchlings and migrating across vast expanses of open ocean, loggerhead turtles return as adults to nest on the same stretch of coastline where they themselves hatched, a behavior known as natal homing [9, 12, 18–21]. Natal homing in sea turtles appears to be accomplished largely through the mechanism of geomagnetic imprinting, in which turtles learn the magnetic field of their home area when young and use this information to return years later as adults [10–12]. Geomagnetic imprinting and magnetic navigation back to the natal beach are possible because Earth's magnetic field varies predictably across the globe [22, 23]. Thus, most coastal areas are marked by different magnetic signatures (Figure 1) [10, 11], which turtles can detect because of their ability to perceive specific elements of Earth's magnetic field, such as intensity and inclination [24–26].

Geomagnetic imprinting and magnetic navigation have interesting but largely unexplored implications for the genetic structure of populations. In many parts of the world, the geomagnetic field varies more from north to south than it does from east to west (Figure 1). Consequently, the geographic distance between two nesting beaches is not a reliable predictor of the magnetic difference between them. Thus, if turtles do indeed locate their natal beaches by returning to the magnetic signature on which they imprinted, then the potential for navigational errors arises whenever two different nesting beaches have very similar magnetic fields. Under such conditions, geomagnetic imprinting predicts that within a given oceanic region, populations of turtles nesting on beaches with similar magnetic fields should be genetically similar and populations of turtles nesting on beaches with different magnetic fields should be genetically distinct. Moreover, this pattern of geomagnetically mediated population structure might persist regardless of either the geographic distance between two nesting areas or their environmental characteristics.

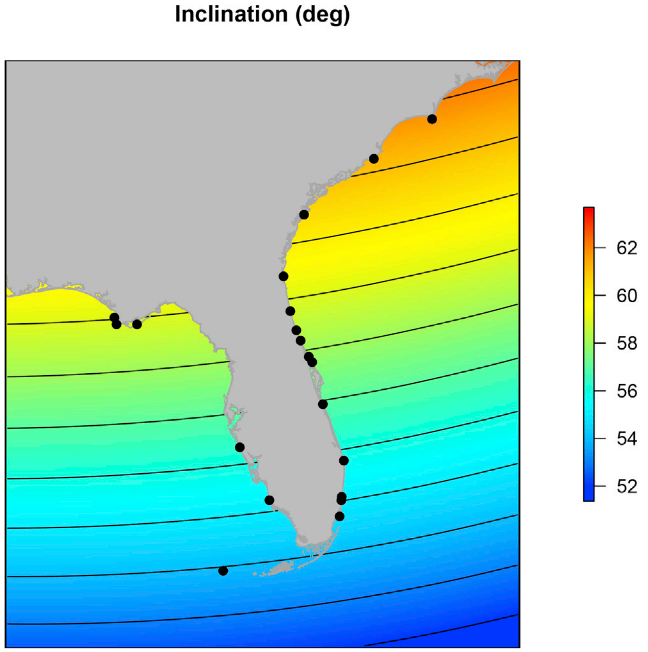

Figure 1. A Map Showing Isolines of Magnetic Inclination Angle along the Southeastern United States Coastline and the Locations of the 20 Nesting Beaches Included in the Analyses

Inclination angle refers to the angle at which magnetic field lines intersect Earth's surface; it varies between 0° at the geomagnetic equator and 90° at the magnetic poles. In this map, each black line represents an isoline of an inclination angle (i.e., a line along which an inclination angle is constant). Adjacent isolines represent increments of 1°. Because the coastline trends north-south and magnetic isolines trend east-west, each area on the Atlantic coast has a different inclination angle and thus a different magnetic signature. Evidence suggests that sea turtles use these magnetic signatures to return to nest on their natal beaches through a combination of geomagnetic imprinting and magnetic navigation [10, 11]. Intensity isolines are not shown, but the pattern is similar to that of inclination isolines [12]. Each black dot represents one of the 20 nesting beaches included in our analyses. Note that some nesting beaches on opposite sides of the Florida peninsula are close to the same isoline and therefore have similar magnetic signatures. As a result, a returning turtle might mistakenly nest on a beach that has the "correct" magnetic field but is actually far from its natal location.

To investigate the hypothesis of isolation by navigation, we analyzed data from an extensive study of loggerhead turtle population genetics [9] in which mtDNA samples were obtained from 834 nesting females across 20 different locations along the southeastern US coast (Figure 1). We extracted F_{ST} values from the reported pairwise comparisons between each possible combination of nesting beaches. F_{ST} is a widely used metric of genetic differentiation that ranges from zero to one, with low values indicating genetic similarity and high values indicating genetic differentiation.

The magnetic field at any location on earth can be described by a field intensity and an inclination angle (the angle that the field lines make with respect to Earth's surface), both of which turtles detect [24, 25]. We calculated a historical average of the magnetic intensities and the magnetic inclination angles that have existed at each of the 20 nesting beaches for the last 425 years and used these data to calculate the magnetic distance between each possible combination of nesting beaches. For the same combinations of beaches, we also calculated (1) the shortest possible oversea distance (i.e., the minimal distance a sea turtle would have to swim to travel from one location to the other) and (2) the environmental distance. Environmental distance describes variation in the environment between nesting beaches and incorporates 21 environmental variables (Table S1), including sea surface temperature, ocean primary productivity, and 19 other standard bioclimatic variables (e.g., annual mean temperature, annual precipitation).

Analyses revealed a striking relationship between genetic differentiation, as estimated by F_{ST}, and spatial variation in Earth's magnetic field (Figure 2). Populations of turtles nesting at beaches with similar magnetic fields tended to be genetically similar; nesting populations at beaches marked by larger differences in magnetic fields had greater genetic differences. Indeed, multiple matrix regression with randomization [27–29] revealed a highly significant relationship between spatial variation in Earth's magnetic field and F_{ST} but found no effect of geographic distance or environmental distance (Table 1). In other words, the difference between the magnetic fields at two nesting beaches was a strong predictor of the genetic differentiation between the turtle populations that nest in the two locations, regardless of the geographic proximity of the nesting beaches or their environmental similarities. Moreover, bootstrap confidence intervals for each regression coefficient (see STAR Methods) show that magnetic distance had a significantly stronger effect on genetic differentiation than did either geographic or environmental distance when all three are considered together (Table 1).

These results provide strong evidence that spatial variation in Earth's magnetic field influences spatial genetic variation in loggerhead turtles through a process most likely mediated by geomagnetic imprinting and magnetic navigation. A plausible interpretation of the findings is that, because some geographically separated beaches have similar magnetic signatures, adult females searching for the magnetic signatures of their natal beaches sometimes nest mistakenly on beaches located elsewhere that also have the "correct" magnetic field. Consistent with this possibility, some loggerheads nest in widely separated locations during their lifetimes, including sites on both the east and west coasts of Florida [30].

The concept of isolation by navigation, in which a navigational process such as geomagnetic imprinting drives population genetic structure, is fundamentally different from isolation by environment. In the latter, the environmental characteristics associated with genetic differentiation are intrinsically coupled to physiology, survival, and fitness; for example, in sea turtles, air temperature and rainfall influence embryonic development [31–34], primary production in the ocean determines food availability [35], and water temperature influences nesting behavior [36, 37]. By contrast, slight differences in Earth's magnetic field, as occur in different geographic locations, have no known effects on either ecosystems or physiology, with the single exception of the processes involved in magnetic navigation. For this reason, the relationship we observe between spatial variation in Earth's magnetic field and genetic differentiation cannot be attributed to isolation by environment, but instead must be considered the result of a separate, independent driver of population structure arising from a navigational strategy. This concept may be

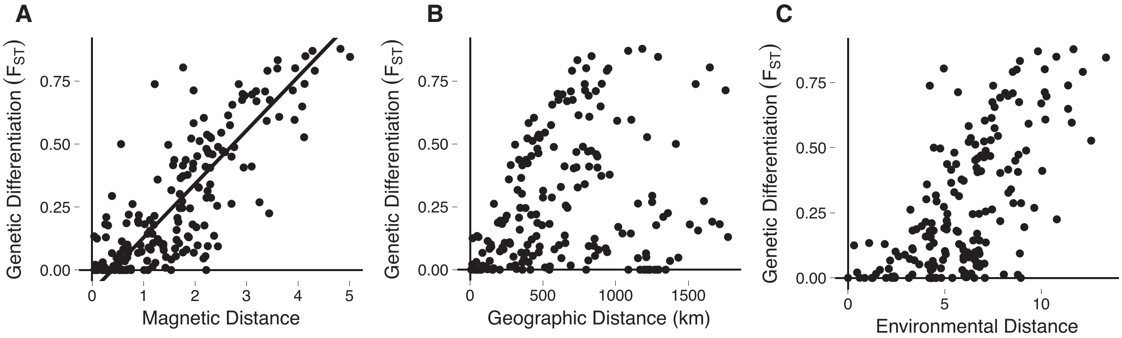

Figure 2. Regression Analyses Showing the Relationship between F_{ST} and the Magnetic Distance, the Geographic Distance, and the Environmental Distance

Each data point represents a pairwise comparison between two nesting beaches with the genetic differentiation between nesting beaches on the y axis and the magnetic, geographic, or environmental distance between the nesting beaches on the x axis.

(A) There is a strong positive relationship between magnetic distance and genetic differentiation (p = 0.001); nesting beaches with similar magnetic fields harbor populations of turtles that are genetically similar, while nesting beaches with different magnetic fields are home to populations of turtles that are genetically distinct.

(B and C) By contrast, no significant relationship is observed between genetic differentiation and either geographic distance (B) or environmental distance (C) (p = 0.533 and p = 0.185, respectively). Moreover, the 95% bootstrap confidence intervals of each regression coefficient indicate that magnetic distance has a significantly stronger effect on genetic differentiation than do geographic and environmental distance (Table 1).

p values were calculated with multiple matrix regression with randomization (MMRR) that incorporated all three distance metrics together and used 1,000 permutations (Table 1). In addition, we used the results from all seven possible models (Table S2) to partition the variation in genetic differentiation explained by the full model (Table S3). See also Figure S1.

important not only for sea turtles, but also for other animals that use magnetic positional information in navigation [38–41].

Although our results provide genetic evidence for geomagnetic imprinting, it is not yet possible to identify with certainty the exact magnetic parameter(s) that turtles use to identify their natal beaches. The most likely candidates appear to be intensity, inclination, or both together [10, 11]. We note that if intensity and inclination are considered separately and analyses are carried out in which each is used as the sole basis for magnetic distance between beaches, then strong relationships are found between each magnetic parameter and genetic differentiation (Figures S1A and S1B). Although it is tempting to conclude that sea turtles imprint on both parameters, an important caveat is that intensity and inclination vary together across the globe, and particularly along the Florida coastline. For this reason, our multivariate analysis used a single metric of magnetic distance that incorporates both inclination and intensity in order to account for the collinearity between them. Moreover, due to the nature of Earth's magnetic field, intensity and inclination are also inherently coupled to other geomagnetic parameters such as horizontal and vertical intensity. Thus, no conclusion can be drawn yet about which parameters of Earth's magnetic field are of the greatest importance.

Similarly, our results do not imply that geomagnetic imprinting and magnetic navigation to natal beaches are the sole determinant of sea turtle population structure. The mechanisms that underlie spatial genetic variation are complex; thus, numerous factors are likely important. For example, even if two nesting beaches have similar magnetic fields, strong ocean currents or other environmental barriers might impede movement between the two and lead to greater genetic differentiation than would be expected through magnetic navigation alone [42]. Conversely, if a population bottleneck or founder effect results in reduced genetic variation across a broad geographic region, then nesting beaches with distinct magnetic fields might harbor genetically similar populations, even though the two locations should, in principle, be easily distinguished by magnetic signatures.

Additionally, although our multivariate analysis found no significant relationship between environmental distance and genetic differentiation (Table 1), we note that the trend is in the expected direction when environmental distance is considered alone. In other words, genetic differentiation between nesting beaches tends to increase with environmental distance (Figure 2C). Environmental factors are indeed critical to success at a nesting beach; both temperature and humidity are known to influence embryonic development [31–34]. Furthermore, at least some evidence suggests that thermal differences between nesting beaches might promote local adaptation under certain conditions [43]. Thus, the possibility remains that environmental distance might affect population structure of sea turtles in the southeastern United States, even though our analysis failed to detect an effect.

Another intriguing aspect of using magnetic navigation to accomplish natal homing is that Earth's field changes over time; this can cause the magnetic signatures that mark natal locations to drift along the coast and might lead to navigational errors. Several studies, however, have revealed that typical rates of field change are compatible with geomagnetic imprinting [10, 11, 44].

Regardless of these considerations, our results provide a powerful, independent new line of genetic evidence for geomagnetic imprinting in sea turtles. In addition, the findings reveal a previously undescribed process that can influence population genetic structure: isolation by navigation. The discovery that spatial variation in Earth's magnetic field shapes the population

Table 1. Results from the Full Model Using Magnetic, Geographic, and Environmental Distance Together to Predict Genetic Differentiation

Multiple Matrix Regression with Randomization (1,000 Permutations)			
Parameter	Estimate	Confidence Interval	p Value
intercept	−0.008	−0.073 to 0.061	1.00
magnetic distance	0.351	0.280 to 0.421	0.001
geographic distance	0.014	−0.029 to 0.054	0.533
environmental distance	−0.090	−0.205 to 0.033	0.185
r^2 = 0.670, F = 125.6, p = 0.001, n = 190			

Multiple matrix regression with randomization (MMRR) revealed a significant effect of magnetic distance on genetic differentiation but failed to detect an effect of either geographic or environmental distance when all three were considered together. In addition, bootstrap confidence intervals for each regression coefficient indicate that magnetic distance had a significantly stronger effect on genetic distance than did either geographic or environmental distance. See STAR Methods for details on MMRR and about how bootstrap confidence intervals were calculated.

structure of a major sea turtle rookery and the inference that magnetic navigation and geomagnetic imprinting can play a role in genetic differentiation are likely relevant to numerous long-distance migrants, including diverse fish, reptiles, birds, and mammals [13–17, 40, 41, 45].

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- QUANTIFICATION AND STATISTICAL ANALYSIS
    - Multiple Matrix Regression with Randomization
    - Bootstrap Confidence Intervals for Regression Coefficients
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SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure and three tables and can be found with this article online at https://doi.org/10.1016/j.cub.2018.03.022.

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AUTHOR CONTRIBUTIONS

J.R.B. and K.J.L. formulated the hypothesis, J.R.B. conducted the analyses, and J.R.B. and K.J.L. wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Distance matrices for geographic, environmental, and magnetic distances	This study	https://doi.org/10.17632/5kk6gzvvzr.1
Software and Algorithms		
R Version 3.3.2	R Core Team [1]	www.r-project.org
ArcMap 10.5.1	ESRI [2]	https://www.esri.com/en-us/home
Other		
Estimates of genetic differentiation	Shamblin et al., 2011 [3]	https://link.springer.com/article/10.1007%2Fs00227-010-1582-6
Mean sea surface temperature data	NOAA OISST v2 [4]	https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html
Net primary productivity estimates	Ocean Productivity	https://www.science.oregonstate.edu/ocean.productivity/
Bioclimatic data	WorldClim [5]	http://www.worldclim.org/
Geomagnetic field parameter estimates	IGRF-12 [6]	https://ngdc.noaa.gov/geomag-web/

CONTACT FOR REAGENT AND RESOURCE SHARING

Requests for further information should be directed to and will be fulfilled by the Lead Contact, J. Roger Brothers (jroger.brothers@gmail.com).

METHOD DETAILS

To estimate genetic differentiation we extracted previously reported F_{ST} values from pairwise comparisons between each possible pairing of 20 nesting beaches across the southeastern U.S.A. [9]. For the same combinations of nesting beaches we also calculated the geographic, environmental, and magnetic distances between each pair (see below) and scaled these distance metrics by dividing each observation by the mean of its group (i.e., geographic, environmental, or magnetic distance).

Geographic Distance

To calculate the shortest possible oversea distance between nesting beaches, we used ArcMap 10.5.1 [46]. The goal was to determine the shortest distance that a turtle could swim in order to travel from one nesting beach to another, rather than the shortest distance a crow could fly. To accomplish this, we used the USA Contiguous Albers Equal Area Conic projection, which minimizes distortion for broader geographic areas, and implemented a processing mask over the continental United States to limit the analysis to marine locations. We then used the Path Distance tool with 500-m grid cell resolution to calculate the shortest distance from one nesting beach to all 19 other beaches. We then iterated across nesting beaches to calculate the shortest oversea distance between all possible pairs of beaches.

Environmental Distance

To quantify the environmental differences between nesting beaches we compiled data for 21 environmental variables (Table S1) at each nesting beach. We then scaled each variable to have unit variance, centered it around zero, and incorporated all 21 into a principal components analysis (PCA). We then calculated the environmental distance between each possible combination of nesting beaches as the Euclidian distance between each pair along the resulting PCA axes. The analysis included 30-year averages (1970-2000) for 19 standard bioclimatic variables (Table S1) at each nesting beach, which we extracted from the WorldClim database [47]. We also included mean sea surface temperature during the nesting season (May, June, and July) averaged over 35 years of data (1981-2016) from NOAA's Optimum Interpolation Sea Surface Temperature database version 2 at locations just offshore from each nesting beach [48]. For the same offshore locations we included mean ocean productivity during the nesting season averaged over 13 years of data (2003-2016) from the Vertically Generalized Production Model, which incorporates MODIS data products to estimate net primary productivity [49].

Magnetic Distance

Finally, we calculated the magnetic distance between nesting beaches using 425 years of magnetic field data from the *gufm1* model (years 1590-1900) and the International Geomagnetic Reference Field model-12 (years 1900-2015) [50, 51]. First, we calculated the average inclination angle and the average magnetic field intensity at each nesting beach, centered and scaled the values as done previously with the environmental variables, and incorporated both magnetic parameters into a PCA. We then calculated the magnetic distance between each possible combination of nesting beaches as the Euclidian distance between each pair along the resulting PCA axes. This method allowed us to account for the strong collinearity between inclination angle and intensity, and look for a relationship between genetic differentiation and Earth's magnetic field without regard to the specific magnetic parameters involved.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were done using R Version 3.3.2 [52].

Multiple Matrix Regression with Randomization

We used multiple matrix regression with randomization (MMRR) with 1,000 permutations to quantify any correlation between genetic differentiation (F_{ST}) and each of the three distance metrics. MMRR is an extension of mantel analysis that uses randomization during significance testing to account for the non-independence that is inherent to distance matrices [27–29].

To account for potential collinearity between magnetic, geographic, and environmental distance, our findings are based on a multivariate analysis that includes all three together. We also considered the six other possible models including those that look at each possible combination of two distance metrics, and those that use each distance metric alone to predict genetic differentiation (Table S2). We then used the results from the entire suite of seven models to partition the variation in genetic differentiation that is explained by the full model [53], an approach that provides some insight into the relative importance of each distance metric (Table S3).

Bootstrap Confidence Intervals for Regression Coefficients

To compare the effect sizes of each of the three distance metrics on genetic differentiation, we constructed bootstrap confidence intervals for each regression coefficient in the full model. To accomplish this and retain potential correlation structure among the residuals, we constructed a matrix of residuals from the model, organized by nesting beach. Then, within each of 10,000 iterations, we used the predicted F_{ST} from our model and a random permutation of the residual matrix to calculate simulated F_{ST} values before refitting the full model. The variation in the coefficient estimates across each of these simulations can be used to generate confidence intervals and evaluate the relative effect size that each distance metric has on genetic differentiation.

DATA AND SOFTWARE AVAILABILITY

The three distance matrices (geographic, environmental, and magnetic) that we generated and used in our analyses have been deposited in the Mendeley Data repository (https://doi.org/10.17632/5kk6gzvvzr.1). The F_{ST} values that we used to estimate genetic differentiation are available in Shamblin et al. [9]. All of the variables we included in both the magnetic and environmental distance calculations are from publicly available databases, which are listed in the Key Resources Table.